Reproductive parameters of female orangutans (Pongo pygmaeus wurmbii) 1971–2011, a 40-year study at Tanjung Puting National Park, Central Kalimantan, Indonesia

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Reproductive parameters of female orangutans (*Pongo pygmaeus wurmbii*) 1971–2011, a 40-year study at Tanjung Puting National Park, Central Kalimantan, Indonesia

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Abstract This study presents reproductive parameter data gathered by direct observation over a 40-year period (1971–2011) of the provisioned free-ranging population of orangutans at Camp Leakey in Tanjung Puting National Park, Central Kalimantan, Indonesia. Age at first reproduction, interbirth interval (IBI), sex ratio at birth, and infant mortality for 19 female orangutans (11 first-generation wild-born ex-captive mothers and 8 second-generation mothers) are included in this analysis. Age at first reproduction among the first-generation mothers was similar to that among wild orangutans, while second-generation mothers had a significantly earlier age at first reproduction. IBIs were similar among first- and second-generation mothers and were significantly shorter than those recorded in studies of wild orangutan populations. There was an expected male-biased sex ratio at birth and a slightly higher than expected rate of infant mortality when compared to wild populations. Infant mortality was primarily seen among second-generation mothers who gave birth before the age of 12, and among first births of some first-generation mothers. These results lend support to the ecological energetics hypothesis, which predicts that increased diet quality leads to a faster rate of reproduction.

Keywords Orangutans · Life history · Reproductive parameters · Interbirth interval · Rehabilitation · Mortality rates · Age at first reproduction

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Introduction

Wild orangutans (genus *Pongo*) have the slowest life histories of any primate taxon (Galdikas and Wood 1990; Knott 2001). With their long interbirth intervals (IBIs), late age at first reproduction, and long life expectancy, orangutans demonstrate extreme values on the spectrum of mammalian life histories (Galdikas and Wood 1990; Knott 2001; Wich et al. 2004). Studying these values and the ecological contexts within which they occur is useful for testing theories that seek to explain the evolution of life history patterns among primates and other mammals (Purvis and Harvey 1995; Kappeler and Pereira 2003; Sibly and Brown 2007). Furthermore, because of their close genetic and evolutionary relationship to humans, documenting orangutan life history is useful for identifying derived features of human life history (Hawkes and Paine 2006).

Comprehensive studies of wild orangutan life history parameters require long-term fieldwork and continuous tracking of identified individuals. Because of this, life history data on orangutans are rare compared to other primate species (Kappeler and Pereira 2003). What data there are suggest varying reproductive rates between Bornean and Sumatran orangutan populations. Wild Sumatran orangutans, who live in more fruit-productive forests (Marshall et al. 2009; Wich et al. 2011) and experience less nutritional stress (Wich et al. 2006) relative to Bornean orangutans,

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have the latest ages at first reproduction and the longest IBIs of all orangutans (Wich et al. 2004). Within Borneo, there is some evidence that *Pongo pygmaeus morio* populations experience the highest degree of nutritional stress and have the shortest IBIs (Wich et al. 2009; Morrogh-Bernard et al. 2009), while *P. p. wurmbii* experience a mid-range level of nutritional stress and have mid-range IBI lengths (Galdikas and Wood 1990; Knott 2001) relative to *P. p. morio* in the east and Sumatran orangutans.

Wich et al. (2004) argue that these intertaxon variations can be explained by the ecological life history hypothesis, which speculates that increased levels of high-quality food in orangutans' diets allow for reduced overall mortality, which thus leads to a slower life history and the allocation of energy towards growth and maintenance rather than reproduction. Key to the ecological life history hypothesis is the idea that these differences in life history evolve over long time periods and become intrinsic to the species. However, studies of captive orangutans (e.g., Anderson et al. 2008; Wich et al. 2009) have not demonstrated slower life histories between Sumatran and Bornean orangutans. Geographic variations in orangutan behavior, morphology, and life history may therefore be better explained by differing immediate factors such as phenotypic plasticity, predation pressure, degree of arboreality, and/or ease of disease transmission among different orangutan populations (Wich et al. 2004; van Schaik et al. 2009).

Within species and subspecies, life history parameters can also be used as a means of establishing interpopulation differences and comparing the effects of differing environmental conditions on populations of orangutans (Wich et al. 2004; Anderson et al. 2008). Correlations between a population's life history parameters and factors relating to its environment have been observed across taxa. In primates, capuchin monkey (*Cebus capucinus*) populations demonstrated a negative correlation between mean IBI length and rainfall amount (Fedigan et al. 2008). Capuchin females had significantly shorter IBIs during very wet periods, when there was a higher availability of food resources (Fedigan et al. 2008). For chimpanzees (*Pan troglodytes*), female life history data from Taronga Park Zoo demonstrate that this naturally breeding population of captive chimpanzees had a significantly earlier mean age at first birth and a significantly shorter mean IBI than chimpanzees living in the wild at Mahale or Gombe (Nishida et al. 2003; Littleton 2005). These differences are thought to be associated, in part, with differences in the nutritional status of the two populations (Littleton 2005); captive females at Taronga likely experienced better nutritional conditions than their wild conspecifics, and thus a higher rate of reproduction.

These interpopulation differences in species reproductive rates are consistent with the ecological energetics hypothesis. This hypothesis predicts that higher-quality diets allow individuals to allocate more energy towards reproduction, thus increasing their reproductive rate (Knott 2001, 2009). Therefore, based on this hypothesis, it would be expected that orangutan populations that experience the greatest consistency of availability of high-quality foods would have significantly earlier ages at first reproduction and shorter IBIs than orangutan populations that are more often forced to rely on low-quality fallback foods such as bark. Studies that have compared the reproductive parameters between *Pongo pygmaeus* and *Pongo abelii* populations living under similar ecological conditions (captivity: Anderson et al. 2008; Wich et al. 2009) have found greater evidence in support of the ecological energetics hypothesis than the ecological life history hypothesis. It seems that improving the nutritional condition of orangutans lowers ages at first reproduction and shortens IBIs to the extent that the apparent differences between *P. pygmaeus* and *P. abelii* are no longer observed.

Emerging evidence suggests that this same pattern can be seen when comparing the reproductive parameters of wild orangutan populations with those of provisioned free-ranging ex-captive populations (Kuze et al. 2012). Wild orangutans are individuals who developed from birth to independence with their biological mothers and who have never received food provisioning or care from humans. Unlike some wild chimpanzee populations, no wild orangutan populations are known to have received food provisioning for the purpose of habituation. Provisioned free-ranging ex-captive orangutans, on the other hand, are orangutans who were born in the wild but have since spent varying amounts of time under the direct care of humans—before and/or during their time at an orangutan rehabilitation center where they are cared for by humans and then eventually returned to the wild. Upon their release back to the wild, these ex-captive free-ranging wild-born orangutans receive daily food provisions (usually from the organizations responsible for their rehabilitation), so as to ensure that they receive adequate levels of nutrition and are able to offset such phenomena as a lack of proper foraging skills and/or higher population densities around release sites. Second-generation provisioned orangutans are those whose mothers were wild-born ex-captive rehabilitants, and thus, although these second-generation orangutans were raised by their biological mothers in the wild, they partake in the post-release provisioning program.

Orangutans living at the Sepilok Orangutan Rehabilitation Centre in Sabah, Malaysia, are members of a free-ranging wild-born ex-captive provisioned orangutan population. Kuze et al. (2008, 2012) showed that these orangutans demonstrated a low mean age at first reproduction, a low ratio of males to females at birth, and a high rate of infant mortality relative to wild orangutan populations, such as those found at Gunung Palung and Tanjung Puting (Galdikas and Wood

1990; Knott 2001; Knott et al. 2009). Interestingly, however, Kuze et al. (2008, 2012) found that the IBI of rehabilitated orangutans at Sepilok (6.2 years) was comparable to that of wild populations of the same subspecies (*P. p. morio*) at Kutai National Park (6.1 years, as reported in Wich et al. 2004; 2009). Many of the differences in observed life history parameters between this population of provisioned *P. p. morio* and other wild—unprovisioned and thus likely nutritionally stressed—populations of Bornean orangutans can be explained by the ecological energetics hypothesis.

Data collected on wild-born ex-captive rehabilitant orangutans at Camp Leakey in Tanjung Puting National Park, Central Kalimantan, Indonesia, satisfy the criteria necessary to derive meaningful life history statistics. These orangutans have been monitored continuously with written records on a daily basis for 40 years by a single principal investigator, the first author, and her assistants, students, and associates. This record is unparalleled for any free-ranging orangutan population in Borneo.

This orangutan community at Camp Leakey is a unique population of orangutans. Unpublished behavioral and paternity data show that they are almost completely isolated from the surrounding wild population (Galdikas, in preparation). This social and genetic isolation, and the fact that they are provisioned on a daily basis, creates a "natural experiment" in which a population of orangutans are freed from certain normal ecological constraints. Furthermore, the fact that this population has been so closely monitored for such a long time (40 years) means that a thorough analysis of their reproductive parameters—age at first reproduction, IBI, infant mortality, and sex ratio at birth—is possible. This analysis could shed light on the effects that ecological conditions have on orangutan reproduction and life history patterns.

Methods

Study site and subjects

Camp Leakey and the surrounding forest (latitude 111°57′ to 112°1′E; longitude 2°45′ to 2°48′S) in Tanjung Puting National Park was the site of Kalimantan's (Indonesian Borneo) first orangutan rehabilitation program, established in 1971. Tanjung Puting National Park is located in the province of Kalimantan Tengah (Central Indonesian Borneo). Although rehabilitation and release no longer take place at this location, Camp Leakey remains an active research site. Within the Camp Leakey study area, there are wild orangutans (*Pongo pygmaeus wurmbii*) as well as rehabilitated orangutans and the first and second generations of their offspring. Ninety orangutans were released at Camp Leakey between 1971 and 1985, with the sex ratio being approximately 50:50. All the released wild-born rehabilitant orangutans that were genetically tested are *P. p. wurmbii*. This correlates with provenience data collected at the time of confiscation, as well as the actual location that confiscation occurred. There may be one possible exception, a female confiscated outside Central Indonesian Borneo, who might come from West Borneo.

The orangutans in the Camp Leakey area are provisioned daily with milk and fruit at a feeding platform supervised by Galdikas and/or long-term local field assistants. After release, wild-born ex-captive orangutans are free to attend the daily feedings or not. The orangutans who come to the feeding platform consist of wild-born ex-captive females and their offspring, as well as a few released males and male offspring of released females. Occasionally, a wild orangutan will also attend the feeding platform and/or visit Camp Leakey. However, this is not a regular occurrence; <5 % of all feedings are attended by wild orangutans. Depending on the availability of high-quality wild foods in the forest, anywhere from 0 to as many as 25 orangutans attend the feeding platform or visit Camp Leakey on any given day.

This study focuses on 19 females (see Table 1) who are either wild-born ex-captive orangutans themselves ($n = 11$) or the offspring of wild-born ex-captive females ($n = 8$). These particular 19 females were frequent visitors to the feeding platform and to Camp Leakey. As such, their reproductive histories have been the most closely monitored of all of the females in the study area and surrounding forest.

Data collection

Data were recorded daily by Galdikas and local field assistants, and are based on direct continuous long-term observation, not hearsay or incomplete records (e.g., Yeager 1997; Kuze et al. 2012). Four primary reproductive parameters are included in this analysis. These parameters are: age at first reproduction, IBI, sex ratio at birth, and infant mortality.

The ages of the first generation of rehabilitated wild-born orangutans at Camp Leakey are based on estimates made when they were first brought into Camp Leakey's rehabilitation program, most as infants and juveniles. Age estimates were made based on deciduous dentition and weight measurements, as well as behavioral observations. The ages of the second generation of orangutans at Camp Leakey have been established by Galdikas and local assistants based on systematic observation around the Camp Leakey study area and the daily feedings. These dates are frequently known to within a few days, and in three cases, the first author actually witnessed the births.

Daily records have been kept of all orangutans encountered around camp, in the study area, and at the feeding platform each day since 1971. When a new infant

Table 1 Offspring of rehabilitated females and their daughters, 1971–2011

No.	Mother		Offspring				
	ID	Age at first reproduction	ID	Birth year	Sex	Year of death	Notes
1	A	16	A1	1981	M	1985	
2			A2	1986	F		
3			A3	1992	M		
4			A4	1999	F		
5			A5	2004	M		
6	A2[a]	13	A2.1	1999	F		
7			A2.2	2005	M		
8	B	16	B1	2000	F		
9			B2	2007	M		
10	C	14	C1	1989	M		
11			C2	1996	F		
12			C3	2002	M		
13			C4	2007	F	2010	
14			C5	2011	M		
15	C2[a]	13	C2.1	2009	M		
16	D	14	D1	1987	F		
17			D2	1994	M		
18			D3	1999	M		
19			D4	2003	M		
20			D5	2008	F		
21	D1[a]	12	D1.1	1999	F		
22			D1.2	2004	F		
23			D1.3	2010	F		
24	E	12	E1	1985	M		Died as an adolescent
25			E2	1990	F		
26			E3	1995	M		
27			E4	2001	M		
28			E5	2007	F		
29	E2[a]	11	E2.1	2001	M	2002	
30			E2.2	2004	F	2005	
31			E2.3	2006	F	2007	
32			E2.4	2008	F		
33	F	15	F1	1977	M	1977	
34			F2	1978	F		
35			F3	1984	M		
36			F4	1987	M		
37			F5	1991	M	1991	F died in 1991 (thus, so did F5)
38	F2[a]	11	F2.1	1989	M	Stillborn	
39			F2.2	1990	F	1991	
40			F2.3	1993	M		F2 never conceived again after nearly dying in 1997
41	G	14	G1	1983	F		
42			G2	1987	M		
43			G3	1992	M		
44			G4	1997	M	1998	
45			G5	2000	M		
46			G6	2005	M		

Table 1 continued

No.	Mother		Offspring				
	ID	Age at first reproduction	ID	Birth year	Sex	Year of death	Notes
47	G1[a]	13	G1.1	1996	F		
48			G1.2	2000	M		
49			G1.3	2005	M		
50			G1.4	2009	M		
51	G1.1[b]	11	G1.1.1	2007	M	2008	
52			G1.1.2	2011	F		
53	H	14	H1	1983	M	1983	
54			H2	1984	M		
55			H3	1991	M		
56			H4	1996	F		
57			H5	2001	M		
58			H6	2006	F		
59			H7	2011	F		
60	I	14	I1	1987	M		
61			I2	1993	F		
62			I3	2000	M		
63			I4	2004	F		
64			I5	2009	M		
65	I2[a]	13	I2.1	2006	M		
66	J	13	J1	2002	M	2004	
67			J2	2005	F		
68			J3	2010	?		
69	K	14	K1	1983	M		1986–1992, K adopted 2 offspring
70			K2	1994	M		
71			K3	2000	M		
72			K4	2006	M	2008	Killed by wild pig
73			K5a	2009	M		Twin
74			K5b	2009	M	2009	Twin

[a] Second-generation mothers

[b] Third-generation mother

is first noticed, his/her birth date is estimated based on the date that his/her mother was last observed without the infant and the first date that she was observed with the infant, noting the presence or absence of an umbilical chord and placenta. In all cases of infant mortality, the date of death is estimated based on the date that the infant was last observed alive and the first date that he/she was observed dead or his/her mother was observed without the infant. Birth and death dates have been rounded to the nearest year.

Statistical analysis

A total of 74 births were recorded for 19 females at Camp Leakey. Table 1 provides a complete overview of these data. Because of the small sample size of the available data, all statistical analyses used were nonparametric. One female, individual G1.1, is a third-generation mother (the daughter of a daughter of an ex-captive rehabilitant female). However, for the sake of robust statistical analyses, she was included with the second-generation mothers. Because she was raised in the wild and had access to the provisioning platform her entire life, she fits the same profile as the second-generation mothers. It is our hope that in the future, as more data become available, it will be possible to conduct three-way analysis, including third-generation mothers as their own category. In the following analyses, however, she is grouped in with the "second-generation mothers."

For analysis of age at first reproduction, we used a Mann–Whitney *U* test to compare first- and second-generation

mothers. We then used a Kruskal–Wallis one-way ANOVA test to compare our data with published data from other orangutan populations. As a post hoc test, we used Mann–Whitney *U* tests with a Bonferonni correction in order to determine the pairs of populations that differed most significantly. To analyze IBI, we used the Kaplan–Meier nonparametric survival analysis method in order to establish the average IBI lengths of the first- and second-generation mothers at Camp Leakey, as well as the population as a whole. We used a log-rank Mantel–Cox test to look for a significant difference in the IBIs of first- and second-generation mothers. We also used a log-rank Mantel–Cox test to look for a significant difference between the IBIs of the Camp Leakey sample as a whole (first- and second-generation mothers) and those of wild orangutans at Tanjung Puting National Park, as published by Galdikas and Wood (1990). The sex ratio at birth was analyzed by conducting a binomial test comparing the ratio of males to females in our sample with the expected ratio (0.5). We also used a chi-squared analysis to compare the sex ratio at birth of first- and second-generation Camp Leakey mothers, as well as compare all Camp Leakey mothers with published infant sex-ratio data from other populations. We used Pearson's chi-squared test to compare the rate of infant mortality (0–3 years) between first- and second-generation mothers as well as between our sample as a whole and published infant mortality data on other populations.

Results

Age at first reproduction

The age at first reproduction was estimated for the 11 first-generation mothers, and was known for the 8 second-generation mothers. The average age at first reproduction for the entire Camp Leakey population was 13.3 years ($n_{ALL} = 19$, $SD_{ALL} = 1.49$, $range_{ALL} = 11–16$). The first-generation mothers' mean age at first reproduction ($mean_{Gen1} = 14.2$, $n_{Gen1} = 11$, $SD_{Gen1} = 1.17$, $range_{Gen1} = 12–16$) was significantly older than that of the second-generation mothers ($mean_{Gen2} = 12.1$, $n_{Gen2} = 8$, $SD_{Gen2} = 0.99$, $range_{Gen2} = 11–13$) (Mann–Whitney *U* test; $n_{Gen1} = 11$, $n_{Gen2} = 8$, $U = 6.5$, $p < 0.001$). Ages at first reproduction of the first- and second-generation Camp Leakey mothers were each compared to two other orangutan populations for which published data sets are available: Sepilok Orangutan Rehabilitation Center ("Sepilok," Kuze et al. 2008) and wild orangutans at Tanjung Puting National Park ("Wild TPNP," Galdikas, personal observation as published in Tilson et al. 1993). The distribution of age at first reproduction varied significantly across populations (CL Gen 1—Sepilok—Wild TPNP, independent-samples Kruskal–Wallis test, $p < 0.005$; CL Gen 2—Sepilok—Wild TPNP, independent-samples Kruskal–Wallis test, $p < 0.05$). Pair-wise Mann–Whitney *U* tests between populations (CL Gen 1—Sepilok, CL Gen 1—Wild TPNP, and CL Gen 2—Sepilok, CL Gen 2—Wild TPNP) with the alpha value adjusted using the Bonferonni correction ($\alpha = 0.05 \div 2$ tests $= 0.025$) shows significant differences between the mean ages at first reproduction of CL Gen 1 and Sepilok (Mann–Whitney *U* test; $n_{Gen1} = 11$, $n_{Sepilok} = 13$, $U = 29$, $p < 0.01$), and CL Gen 2 and Wild TPNP (Mann–Whitney *U* test; $n_{Gen2} = 8$, $n_{WildTPNP} = 3$, $U = 36$, $p < 0.01$). Table 2 shows the summary statistics of the data used for this analysis.

Table 2 Age at first reproduction

Population	Mean	*N*	SD	Range
All Camp Leakey	13.3	19	1.49	11–16
Camp Leakey first-generation mothers	14.2	11	1.17	12–16
Camp Leakey second-generation mothers	12.1	8	0.99	11–13
Rehabilitant Sepilok (Kuze et al. 2008)	11.6	13	2.3	8–15
Wild Tanjung Puting National Park (Tilson et al. 1993)	15.7	3	0.50	15–16

Interbirth interval

A total of 72 IBIs were recorded among the Camp Leakey population. Of the 74 infants born to 19 females at Camp Leakey, two infants were twins (offspring K5a and K5b; thus their birth data contributes to closing only one IBI), and one infant died shortly after birth when his mother died (mother F, offspring F5). A nonparametric Kaplan–Meier survival analysis of the remaining IBIs yields a mean of 5.5 years ($n = 72$, with 18 censored intervals, SE 0.42). Of these 72 IBIs, 13 were incomplete intervals, meaning that the mother's previous offspring died before the birth of her next. Another two IBIs were highly irregular: one female (mother F2) has yet to conceive again after suffering a near-fatal bowel rupture in 1997 (yielding a censored IBI length of 18 years); and another female (mother K) adopted two young orangutans between the births of her first and second offspring, yielding an IBI length of 11 years. However, removing these incomplete and irregular IBIs from the sample, a nonparametric Kaplan–Meier survival analysis yields the same mean of 5.50 years ($n = 57$, with 17 censored intervals, SE 0.16). When IBI is computed separately for the first- and second-generation mothers, the Kaplan–Meier analysis of first-generation mothers' IBIs yields a mean IBI of 5.35 years for all the data ($n = 52$, SE 0.29, with 10 censored intervals) and a mean of 5.52 years for the completed and regular IBIs ($n = 44$, SE 0.18, with

Table 3 Interbirth Intervals (IBIs)

Population	All intervals				Completed and regular intervals			
	K–M means	*N*	*N* censored	SE	*K–M* means	*N*	*N* censored	SE
Camp Leakey first-generation mothers	5.35	52	10	0.29	5.52	44	10	0.18
Camp Leakey second-generation mothers	5.95 [a]	20	8	1.44	5.45 [a]	13	7	0.38
All Camp Leakey	5.5	72	18	0.42	5.5	57	17	0.16
Wild Tanjung Puting National Park[b]					7.82 [*]	23	11	0.39

* $p < 0.001$

[a] Not significant

[b] (Galdikas and Wood 1990)

10 censored intervals). Kaplan–Meier analysis of second-generation mothers' IBIs yields a mean of 5.95 years for all the data ($n = 20$, SE 1.44, with 8 censored intervals), and a mean of 5.45 years for the completed and regular IBIs ($n = 13$, SE 0.38, with 7 censored intervals). Post hoc analyses comparing the mean IBIs of first- and second-generation mothers reveal no significant difference between the means of all IBIs or those of just the completed and regular IBIs (Mantel–Cox test; all IBIs, $\chi^2 = 0.252$, $df = 1$, $p > 0.05$; completed and regular IBIs, $\chi^2 = 0.031$, $df = 1$, $p > 0.05$). Thus, we consider 5.5 years to be the most accurate mean IBI of the Camp Leakey population.

A Mantel–Cox log rank test comparing the IBI lengths of wild *P. p. wurmbii* in Tanjung Puting National Park (Galdikas and Wood 1990) with the completed and regular IBI lengths of the provisioned *P. p. wurmbii* at Camp Leakey shows that the average IBI of the wild females is significantly longer than that of Camp Leakey's provisioned females ($\chi^2 = 19.83$, $df = 1$, $p < 0.001$). Table 3 provides a summary of this analysis.

Sex ratio at birth

Of the 74 offspring born to the 19 females in our sample, 46 were male, 27 were female, and one is yet to be identified and has therefore been discounted (offspring J3). A binomial test of this ratio ($n = 73$, proportion of males at birth = 0.63) compared to the expected (0.5) shows significance [$(X \geq 46) = 0.017$]. Chi-squared analyses show that the sex ratio at birth of first-generation Camp Leakey mothers does not differ significantly from that of second-generation Camp Leakey mothers ($\chi^2 = 2.002$, $df = 1$, $p > 0.05$). Comparing the entire Camp Leakey sample to published data for Sepilok (Kuze et al. 2012), Sepilok had a significantly lower ratio of males to females (Sepilok sex ratio at birth = 0.07, $n = 27$; Pearson's chi-squared test: $\chi^2 = 23.49$, $df = 1$, $p < 0.001$). When compared to data from captive (zoo) *Pongo* (Singleton and van Schaik 2002), the difference was barely significant, with Camp Leakey again having a higher ratio of males to females than in the zoo (zoo sex ratio at birth = 0.51, $n = 755$; Pearson's chi-squared test: $\chi^2 = 3.854$, $df = 1$, $p = 0.05$). Unfortunately, published sex ratios at birth are not available for any wild population of *P. p. wurmbii*. However, the sex

Table 4 Sex ratio at birth

Population	Proportion of males at birth	*N*
All Camp Leakey	0.63	73
Rehabilitant Sepilok (Kuze et al. 2012)	0.07	26
Captive, zoo (Singleton and van Schaik 2002)	0.51	755
Wild *P. abelii* at Ketambe (Wich et al. 2004)	0.57	28
Wild *P. abelii* at Suaq Balimbing (Singleton and van Schaik 2002)	0.56	25

ratio at birth at Camp Leakey is not significantly different from that of wild *P. abelii* at Ketambe (Wich et al. 2004; $n = 28$, proportion of males at birth = 0.57; $\chi^2 = 0.29$, $df = 1$, $p = 0.65$) or Suaq Balimbing (Singleton and van Schaik 2002; $n = 25$, proportion of males at birth = 0.56; $\chi^2 = 0.32$, $df = 1$, $p = 0.67$). Table 4 gives a summary of the data used in this analysis.

Infant mortality

Sixty-six offspring at Camp Leakey were included in the analysis of infant mortality; one infant who died because his mother died shortly after his birth (mother F, offspring F5), as well as seven infants whose ages had not passed three years, have been discounted from this analysis. The infant mortality rate for all Camp Leakey mothers was 20.0 % (Table 5), with 13 out of 66 infants not surviving past the age of 3 years. The infant mortality rate for first-generation mothers was 14 % ($n = 48$), and 35 % ($n = 18$) for second-generation mothers. Although this difference is not significant (Pearson's chi-squared test, $\chi^2 = 3.5$, $df = 1$, $p > 0.05$), it is striking.

A close examination of our sample shows that, among the first-generation females who lost infants, half of the cases ($n = 3$) were first-borns. Among the second-generation females, there may be a relationship between age at first reproduction and mortality of the first infant: all the females who first gave birth at the age of 11 years ($n = 3$) lost at least their first infant. However, those second-generation mothers who first gave birth at 12 or 13 ($n = 5$) did not lose any infants.

Chi-squared analyses show that the infant mortality rate for all mothers at Camp Leakey is not significantly different from that for captive *Pongo pygmaeus* (21 %, Anderson et al. 2008; $\chi^2 = 0.02$, $df = 1$, $p > 0.05$). However, infant mortality at Camp Leakey was significantly lower than that among the provisioned rehabilitant population at Sepilok (58 %, Kuze et al. 2012; Pearson's chi-squared test, $\chi^2 = 10.62$, $df = 1$, $p < 0.001$), where over half of all infants did not survive past their third year. At Tanjung Puting National Park, over a 40-year period, only two cases of infant mortality among the wild orangutan population were noted: a young male who disappeared during late infancy, and a stillborn female infant (Galdikas, unpublished data). Furthermore, at the Tuanan Orangutan Research Station, no infant deaths among the *P. p. wurmbii* population have been recorded over 8 documented live births since 2003 (van Noordwijk, personal communication).

Table 5 Infant mortality

Population	Infant mortality rate	*N*
All Camp Leakey	0.20	66
Camp Leakey first-generation mothers	0.14	48
Camp Leakey second-generation mothers	0.35	18
Rehabilitant Sepilok (Kuze et al. 2012)	0.58	19
Captive *P. pygmaeus*, zoo (Anderson et al. 2008)	0.21	440

Discussion

Age at first reproduction

The first generation of mothers—those that came to Camp Leakey as orphans—gave birth to their first offspring at a significantly older mean age than the second generation of mothers—those that were born and grew up with their biological mothers at Camp Leakey. There are two conceivable explanations for this difference. First of all, it is possible that, upon entering the rehabilitation program at Camp Leakey, the ages of the first generation of females were overestimated. Photographic records, however, indicate that the opposite may be true: it appears that upon entering the rehabilitation program, female ages were—if anything—underestimated. This would mean that the true mean age at first reproduction of the first-generation females in this data set is actually higher than shown here.

The second explanation for this generational difference may be found in the differing levels of early nutrition received by these two generations of females—the first generation having grown up in the wild and in potentially poor captive conditions prior to entering the rehabilitation program, and the second generation having received a high-quality diet from the daily provisioning throughout their development and maturation. Energetic status during development has been shown to have lasting effects on female human health and reproduction (Ellison et al. 1993; Duncan and Scott 2004). Women who experience high nutritional conditions during development and maturation have earlier ages of menarche and first birth when compared to women who grow up under conditions of nutritional stress (Gluckman and Hanson 2006). Furthermore, level of nourishment has been shown to correlate indirectly with the length of adolescent subfecundity and the consistency of ovarian function among humans (Ellison et al. 1993; Duncan and Scott 2004). Thus, it is likely that among the Camp Leakey orangutans, the second-generation females exhibit an accelerated age at first menarche and a reduced period of adolescent subfecundity due to having experienced consistently high dietary quality throughout their development. The first-generation females, however, likely had a more normal, or even delayed (if their initial ages were indeed underestimated), age at first menarche

and a lengthened period of adolescent subfecundity due to having experienced poor and/or variable dietary quality while living under stressed wild conditions or in poor captive conditions prior to entering the rehabilitation program. This finding is therefore consistent with the ecological energetics hypothesis.

The same factors that have led to the difference in the ages at first reproduction of the first- and second-generation females at Camp Leakey can also explain the discrepancies between wild and rehabilitant populations. The mean age at first reproduction of the second generation of Camp Leakey mothers did not differ significantly from that of the provisioned rehabilitant population of *P. p. morio* at Sepilok, but did differ significantly from that of wild *P. p. wurmbii* in Tanjung Puting National Park. The mean age at first reproduction of the first-generation females, however, was not significantly different from that of the wild Tanjung Puting population. It is likely that this early age at first reproduction seen among the Sepilok and the Camp Leakey second-generation rehabilitant populations is also a direct outcome of regular provisioning. Regular provisioning provides these rehabilitated orangutans with improved nutritional conditions relative to their wild unprovisioned conspecifics. That the first-generation Camp Leakey rehabilitants' age at first reproduction was similar to their wild conspecifics could be explained by the importance of early nutrition in later reproduction: the variable and poor nutritional conditions received in captivity during early development may have outweighed the effects of subsequent positive nutritional conditions on accelerating age at first menarche and reproduction. Until more data are available, however, the full effects of provisioning—and especially the timing of the beginning of provisioning—on age at first reproduction remains unclear.

Interbirth interval

The observed IBI of these provisioned orangutans at Camp Leakey is significantly shorter than the IBI of the wild orangutans of Tanjung Puting National Park (Galdikas and Wood 1990). This finding is consistent with the ecological energetics hypothesis, which indicates that increased levels of high-quality food in a female's diet allow her to allocate more energy to reproduction and thus reproduce at a faster rate, shortening her IBI (Knott 2001). This shorter IBI finding is in contrast, however, to results found by Kuze et al. (2012) at Sepilok. Kuze et al. (2012) calculated a similar IBI among the Sepilok orangutans (6.2 years) to the wild population of the same subspecies at Kutai National Park (6.1 years; as reported in Wich et al. 2004; 2009). This potential difference in response to provisioning—*P. p. wurmbii*'s decreasing IBI versus *P. p. morio*'s IBI that remains consistent with wild data—could be the result of several different-not mutually exclusive-factors, including: differences in provisioning practices or unconsidered differences in environmental ecology between Camp Leakey and Sepilok, or a subspecies difference in reactions to provisioning between *P. p. wurmbii* and *P. p. morio*. The wild *P. p. morio* data, however, are based on small sample sizes and unpublished data, so it is not possible to test for statistically significant differences between the rehabilitant and wild populations. It remains to be seen whether or not this consistency between rehabilitant and wild *P. p. morio* IBI holds as more robust data sets become available.

Anderson et al. (2008) found similar results in their study of life history parameters among zoo orangutans: both captive Sumatran and captive Bornean orangutans had shorter IBIs than in the wild. It is safe to assume that orangutans in zoos are receiving high-quality diets. Thus, we see further IBI evidence for the ecological energetics hypothesis and the high degree of flexibility with respect to reproduction demonstrated by orangutans.

Sex ratio at birth

Sixty-three percent of the offspring born to both generations of provisioned orangutans at Camp Leakey have been males. This skewed sex ratio at birth is significantly different from a theoretically expected sex ratio of 1:1, and can be best explained by orangutan dispersal patterns and the local resource competition hypothesis proposed by Clark (1978).

Many long-term behavioral studies have found evidence of female philopatry and male-biased dispersal among orangutan populations (MacKinnon 1974; Galdikas 1985; Singleton and van Schaik 2002; Knott et al. 2008). Several recent genetic studies have found further evidence in support of the theory that related female orangutans cluster together while males move far from their natal areas (Arora et al. 2010; Morrogh-Bernard et al. 2010; Nater et al. 2011; van Noordwijk et al. 2012). It is clear that provisioned rehabilitant orangutans at Camp Leakey exhibit similar patterns of female philopatry with male-biased dispersal (Galdikas, unpublished data).

The local resource competition hypothesis, originally proposed by Clark (1978), can therefore be applied to the orangutans at Camp Leakey. This population of orangutans satisfy the three key criteria of this theory: (1) female kin remain closely associated socially and spatially for much of their lives, (2) males are not restricted to specific home ranges and often range far from their mothers and sisters, and (3) there is a small, one-of-a-kind area of prolific food supply that is vital for supporting pregnant and lactating females (in the case of Camp Leakey: the feeding platform). Because these three criteria are satisfied, it is advantageous for mothers at Camp Leakey to differentially

produce male offspring who will emigrate from their natal area rather than females who will remain close by and increase feeding competition around the feeding platform. Furthermore, Silk and Brown (2008) found evidence across primate species that male-biased sex ratios at birth are correlated with male-biased dispersal.

Thus, it makes sense that Camp Leakey's male-biased sex ratio at birth is not significantly different from the sex ratio at birth of wild populations of *P. abelii* at Ketambe (Wich et al. 2004) and Suaq Balimbing (Singleton and van Schaik 2002). Singleton and van Schaik (2002) found male-biased sex ratios at birth but female-biased sex ratios among adult orangutans, a phenomenon that can be explained by differential male mortality and/or male-biased dispersal. Unfortunately, no data is available on the sex ratio at birth among wild Bornean orangutans.

The rehabilitated orangutan population at Sepilok exhibited an extremely low ratio of males to females at birth, significantly different from Camp Leakey's sex ratio at birth. Kuze et al. (2008) speculate that this can also be explained by the Trivers and Willard (1973) hypothesis: mothers at Sepilok suffer from low health because of the stress caused by a high degree of gregariousness around feeding platforms and a high level of parasite exposure, and thus they produce a disproportionately high number of daughters to sons. Furthermore, captive *Pongo* also exhibited a significantly different sex ratio at birth from the Camp Leakey orangutans. The sex ratio at birth of captive orangutans more closely approached the theoretically expected value of 0.5, and can likely be explained by the differences in ecological conditions experienced by animals living in captivity (Singleton and van Schaik 2002). More studies are needed, however, in order to firmly establish the effects of provisioning and captivity on sex ratios at birth.

Infant mortality

Social connectivity has been shown to be a major factor in disease transmission among wild infant chimpanzees, with infant mortality rates peaking in correlation with social play rates (Kuehl et al. 2008). The overall presence of infant mortality (among both first- and second-generation mothers) at Camp Leakey may partly be explained by disease transmission around the highly gregarious feeding platform. The rehabilitant orangutans at Camp Leakey are much more gregarious than wild *P. p. wurmbii* populations at Camp Leakey (Galdikas 1985; Galdikas, unpublished data) or at Tuanan Orangutan Research Station (Ashbury, personal observation). Because of the high amount of social contact occurring around the feeding platform, infants are exposed to, and in contact with, peers and other conspecifics more frequently than their wild conspecifics. Thus, disease transmission exacerbated by a high degree of social connectivity should not be dismissed as a causal factor of infant mortality.

Many of the rehabilitant orangutans at Camp Leakey also spend a large amount of time on the ground relative to wild orangutans (Galdikas, personal observation). Crowding and ground dwelling have both been shown to be factors leading to parasitic infections among orangutan populations in Sumatra (Mul et al. 2007). Ground-dwelling habits may also contribute to infant mortality rates at Camp Leakey, as mothers who spend more time on the ground are increasing their own and their infants' vulnerability not just to parasitic infection but also to terrestrial predators such as wild pigs. One such case of predation is known and recorded in this data set (offspring K4). Furthermore, several adult female Camp Leakey orangutans often choose to come into close proximity, and even contact, with research assistants and camp staff, so disease and/or parasite transmission between humans and orangutans may have occurred.

The rate of infant mortality at Camp Leakey was significantly lower than that at Sepilok (Kuze et al. 2008). Kuze et al. (2008) speculate that their extremely high (58 %) observed rate of infant mortality had two possible causes: (1) human rearing causing poor infant care skills, and (2) increased sociality due to provisioning leading to increased aggression and disease transmission. These factors may also be contributing to the infant mortality rate at Camp Leakey, although it is not as extreme as at Sepilok. It could be that other, thus far unconsidered, ecological factors are contributing to the high rate of infant mortality at Sepilok.

The rate of infant mortality at Camp Leakey differed, though not significantly, between the first- and second-generation mothers. It is important, however, to look at not just the rates of infant mortality but also the patterns of infant loss with respect to mothers' ages. The cases of infant death among the first-born offspring of second-generation mothers can likely be explained by these females' early ages at first reproduction. It is possible that in some cases, the second-generation females' ages at first reproduction have been reduced to the extent that they are simply giving birth before they are psychologically and physiologically ready. At only 11 years old, they are still lacking the necessary social and ecological skills, as well as the physical readiness, to gestate, lactate, and then properly raise an infant. As such, the first infants of such young mothers appear to occasionally be born premature (or, as in the case of mother F2, stillborn), and thus unable to cling and suckle properly. This infant helplessness combined with a young mother's lack of problem-solving skills is detrimental to the survival of the first infant. It may be that the similar rate of infant mortality observed among

zoo orangutans can also be correlated with their early ages at first birth (Anderson et al. 2008). A similar phenomenon has been observed among humans: maternal age correlates directly with infant survival (Friede et al. 1987, Fraser et al. 1995). Even when controlling for socioeconomic factors, women who give birth younger face increased risk of adverse outcomes of pregnancy, including prematurity, low birth weight, and infant death (Fraser et al. 1995).

The tendency for a mother to lose her first-born infant was also seen among the first-generation females; half of the cases of infant mortality were first borns. Of the other three cases of infant death, one was a twin (whose twin brother survived), and the other was an exceptional case of an infant killed by a wild pig. Thus, discounting exceptional cases, there appears to be a mortality bias towards first borns, even among the first-generation mothers. This phenomenon may be explained by a delayed acquirement of proper infant-rearing skills by certain females. The trend of higher infant mortality among first borns has also been observed among humans, although the causal factors—namely the role of maternal age and socioeconomic status—remain unclear (Mathews and MacDorman 2008).

Provisioning and the effects of the feeding platform

It is clear that the ecological energetics model outlined by Knott (2001) can be used to explain many of the reproductive phenomena observed among the provisioned rehabilitant orangutans at Camp Leakey. The earlier mean age at first reproduction among the second-generation mothers and the shorter population mean IBI, when compared to wild orangutan populations, are both likely to be primarily a result of the improved nutritional conditions experienced by these provisioned individuals. Provisioning thus decreases within-population feeding competition and increases individual reproductive potential, causing earlier and more frequent reproduction.

It is not only the fact of provisioning but also the method of provisioning that affects orangutan life history parameters at Camp Leakey. Because the orangutans are mainly provisioned once per day at a single location, local resource competition may play a role in shaping birth sex ratios, and social connectivity may play a causal role in infant mortality rates.

Our study does not find support for the ecological life history hypothesis. Where sufficient data are available, it is clear that the reproductive parameters of the provisioned Camp Leakey orangutans differ significantly from those of wild *P. p. wurmbii*, even in the study area that surrounds Camp Leakey. Other studies examining the effects of rehabilitation and provisioning have provided inconclusive and conflicting evidence for the ecological life history hypothesis (e.g., Kuze et al. 2012). It could be that the ecological life history model provides a satisfactory framework for explaining reproductive variation existing on an evolutionary, long-term, interspecific timeframe. Thus, the ecological life history hypothesis may explain the differences in reproductive parameters between Bornean and Sumatran orangutans. However, when explaining variation between populations within species, or across multiple generations within a population, the ecological energetics model provides a less problematic explanatory framework.

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